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POLLINATION STRATEGIES OF ORCHIDACEAE WITH SPECIAL REFERENCE TO INDIA: A REVIEW

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Abstract:

Aesthetically, economically and ecologically significant flowering plant group orchids use several types of pollination strategy for reproductive success. Specially cross-pollinated orchids lure huge number of diverse pollinators by utilizing unique and spectacular deceptive pollination mechanism alongside rewarding mechanism. 1350 reported Indian species distributed across the whole continent and found mainly in the Eastern Himalayas and North Eastern, North West Himalayas, Peninsular India, and Andaman and Nicobar Islands. There are plethora of India based researches on geographical distribution, conservation and diversity, morphology and taxonomy, cultivation and artificial propagation and also economical uses of orchids. But there is significantly lesser amount of reports present especially in Indian perspective about orchid pollination studies. Here we discuss about orchids and their pollinators along with different pollination mechanisms by assembling several available scientific data, photographs, analyses, comparisons, facts etc. reported till to date. Discussions in this review represent a quality overview on current state of orchid pollination specially mentioning about Indian orchid species, their distribution and their

pollinators. This study may be useful and beneficial for the future researchers who are willing to work on orchid pollination biology with a special emphasis on India.

Keywords: *Orchid pollination, deceptive pollination, pseudocopulation, co-evolution, diverse pollinators, distribution, Indian orchids*.

1. Introduction:

The word pollination is simply defined as the process of transfer of male reproductive cell, i.e., pollen grains from male reproductive part of flower (anther) to female reproductive part (stigma). Plants can either be self-pollinated or cross-pollinated. Cross-pollination introduces genetic recombination, variety and variability, species diversity and thus this process is proved to be evolution-friendly. Orchids belong to the family Orchidaceae, the second largest family in flowering plants under order Asparagales, contain approximately 763 genera which include more than 28000 accepted species that are distributed worldwide, particularly abundant in wet tropics (Christenhusz and Byng, 2016). These epiphytic or terrestrial plants have flowers with fascinating coloration, miscellaneous odors, and complex structures, having large specialized part known as labellum and frequently a spur also. Orchids adapt several specialized floral features to attract diverse pollinators mainly bees and flies. Although non-rewarding or deceptive pollination method is a remarkable and unique character of several orchid species, there are other orchids that are known to lure pollinators by rewarding them in different ways (providing nectar, protein-rich pollen, floral oils, several edible floral parts etc.). Both the rewarding and non-rewarding orchids attract their pollinators by giving off olfactory, optic and tactile cues. Orchids and their pollinators often co-evolve. Study of orchid pollination is essential because orchids represent numerous beneficial aspects from economic point of view as well as leave great impacts on ecology and environment. In order to properly conserve and scientifically propagate several endemic and endangered orchid species and their pollinators a thorough knowledge and core idea about orchid pollination biology should be obligatory.

2. *History of orchid pollination*

Still existing orchid species, throughout the world, have a common ancestor which was the most recent, lived in the Late Cretaceous. Around 65.5 million years ago, when the mass extinctions at the Cretaceous-Tertiary boundary took place, a massive radiation of orchids followed shortly after (Zhang *et al*., 2018). According to a study published in the scientific journal *Nature* (Ramírez *et al*., 2007), there is prominent evidence of active orchid-insect interaction explaining the phenomenon of pollination, from the prehistoric period of 15-20 million years ago. Ramirez *et al*. (2007) also reported the evidence of fossilized orchid and its pollinator is in the form of Miocene amber which trapped an extinct species of stingless bee, *Proplebeia dominicana* carrying pollen of a previously unknown orchid taxon, *Meliorchis caribea*, on its wings. Micheneau *et al*., 2009 described the entire history of orchid pollination by separating it into three major time periods:

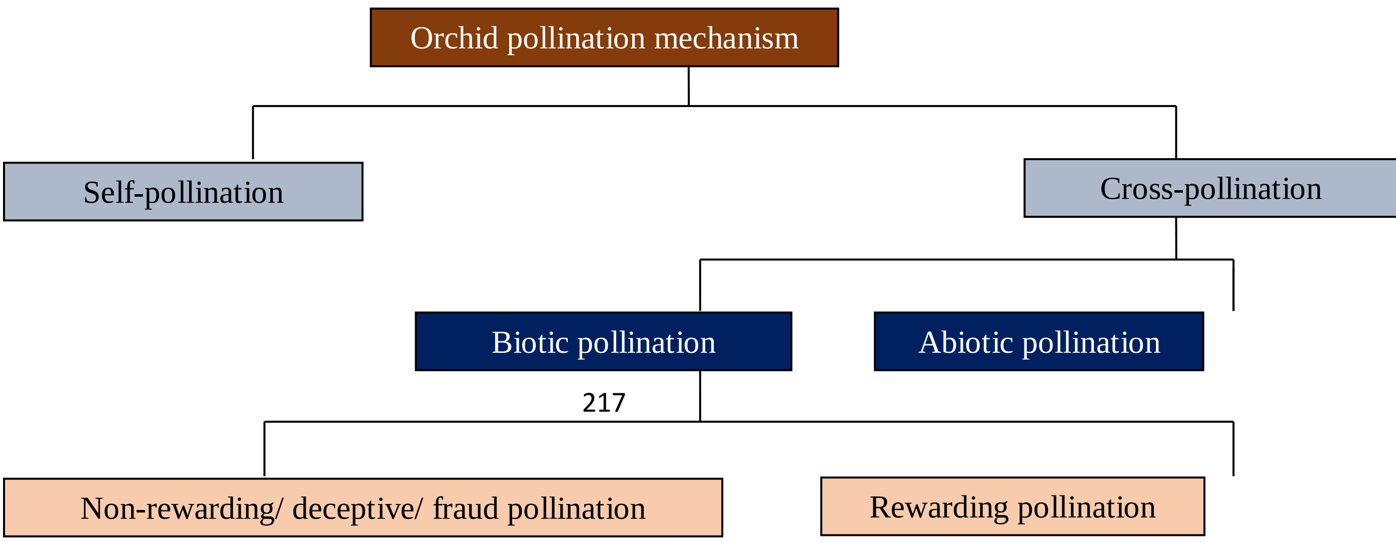
A. From Darwin's era to 1930s: Several botanists including the likes of Bernard de Jussieu and Michel Adanson, around the end of 18th century, enlighten the area of general morphology of orchid flowers. In 1862, Charles Darwin was first to describe about 'pollination mechanisms in orchids' in detail in his book 'On the various contrivances by which British and foreign orchids are fertilized by insects and the good effects of intercrossing'. In 1877, *The various contrivances by which orchids are fertilized by insects*, 2nd edn., was published reflecting Darwin's contemporary Fritz Müller's observations which was mainly focused on tropical orchids (Darwin, 1877). Several scientists, biologists and naturalists from the western world were highly inspired by the works of Darwin and they began to explore new horizon in this fascinating topic of orchid pollination biology, beginning from Darwin's period till 1920s. By the end of this period, the pollination mechanism of the genera *Ophrys* and *Cryptostylis* were discovered from Algeria and south-eastern Australia respectively. This pollination mechanism occurred by the means of pseudo copulation (Correvon and Pouyanne, 1916; Pouyanne, 1917; Coleman, 1927; Micheneau *et al*., 2009).

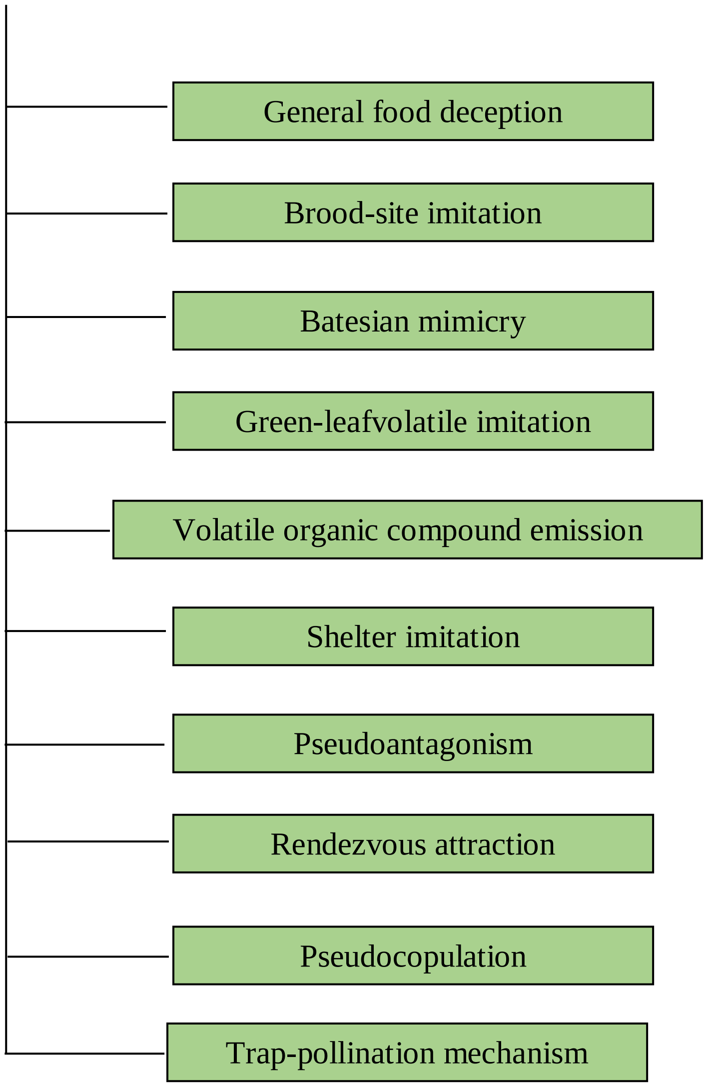
B. 1930s to 1960s: In this time period, the focus of the community of scientists and biologists were gradually shifted from the field of biology related to orchid flowers and their interaction with pollinators to the study of 'cytology and genetics'. In 1966, van der Pijl and Dodson reviewed all the documented observations on orchid-pollinator interactions which was recorded throughout a whole century, in their book *Orchid flowers, their pollination and evolution*, the second classic book of orchid pollination (Pijil and Dodson, 1966). Except themselves, the authors also utilize major recent contributions by R. L. Dressler and B. Kullenberg while writing their book. The area in the orchid pollination syndrome that was mainly presented by this book was the important role of pollinators in case of evolutionary history of family Orchidaceae.

C. From 1960s to the recent times: After a long latent period of nearly 30 years, the interest in pollination biology was manifested with renewed enthusiasm beginning from the end of 1960s. In this time period scientists started to explore pollination biology from several broader aspects such as developmental ecology, evolutionary concepts and models which is also considered as a part of 'biosystematics'(Proctor *et al*., 1996), reproductive biology and also population dynamics. Orchid-pollinator interactions can be measured by the removal and deposition of pollinia. Throughout the entire world a massive amount of quantitative data on orchid pollination and their reproductive success were gathered by many scientists approximately from 1981 to 2004 (Castro and Singer, 2019). These data were recorded based on the works, mainly done in Europe and North America, the Neotropics and Australia and in South Africa. In 1998, a research work about the comparison of reproductive success in 117 temperate and tropical orchids which are both nectariferous and nectarless was done by Neiland and Wilcock. They concluded that reproductive success is much higher in nectariferous orchids than the nectarless species and that's why they observed more fruit setting in case of nectariferous orchids. In 2005, Tremblay *et al*. revealed an elaborated overview of orchid floral biology alongside, sources of variation and the gradual evolution depending upon natural selection and genetic drift, concept of pollination limitation and several statistical analysis on the topic of successful fruit set in the family Orchidaceae. Jersáková, Johnson and Kindlmann, in 2006, showed in their review that orchids emphasis on non-rewarding deceptive pollination mechanism promoting the higher amount of cross-pollination. In 2007, a published article by Ramírez *et al*. first introduced about the fossilized record of orchid-pollinator interaction in the form of amber which unveil a vast horizon of the ancient history and origin of Orchids.

3. Mechanisms of orchid pollination

Orchid pollination mechanisms are highly diverse and complex. An elaborated classification of their pollination mechanisms is as follows:





3.1. Self-pollination:

In case of several orchids, the pollen grains are transferred from an anther to the stigma of the same flower. In insect-scarce environments, self-pollination is considered a potential adaptation mechanism for orchids (Chen *et al*., 2012). Nearly about 5-20% of orchid species use self-pollination mechanism (Calting, 1990).Here we are mainly discussing about four orchid species that are found in India, shows different self-pollination methods. The epiphytic orchid *Holcoglossum amesianum* (Rchb.f.) Christenson has a bisexual flower that twists its anthers 360º contravening the effect of gravity in order to intromit the pollen grains inside its own stigma cavity without any help of pollinators and pollinating medium (Liu *et al*., 2006). At the time of bud development, the saprophytic orchid *Epipogium roseum* (D.Don) Lindl. loses the function of degenerative rostellum which serves as physical barrier providing separation between male reproductive organ (stamens) and the head of the pistil (stigma). As a result, the pollinia are capable to reach and come in contact with stigmatic secretions (Zhou *et al*., 2012). In 2010, Chen and his colleagues carried out a study on the reproductive biology of *Eulophia graminea* Lindl., involving the following steps: collection of seeds from capsules, sown in-vitro, germination of seeds, formation of rhizome, gradually grow into plants, flower development and eventually fruit generation. Thus experimenting for 4 generations they concluded that *E. graminea* possesses an autogamous mating system. After transitioning from solid to liquid state, the anther of *Paphiopedilum parishii* directly falls upon and settles on the surface of the stigma without the assistance of any pollinator, pollinating medium or floral assembly (Chen *et al*., 2012).

3.2. Cross pollination:

In case of numerous orchid species the pollen grains are transferred from an anther of one flower to the stigma of another flower borne on different plants of same or different species. Approximately 60-70% of the total orchid species utilize cross pollination mechanism. Depending upon the various kinds of pollinating agents, the mechanism of cross pollination is of two types. They are as follows:

3.2.1. Abiotic mode of pollination:

Here pollens are transferred by using wind, rain-fall, gravity and secretions. The most prominent example of rain pollinated orchid is *Acampe rigida* (Buch.-Ham. ex Sm.) P. F. Hunt (Tang *et al*., 2014; Fan *et al*., 2012). *Oeceoclades maculate* utilizes abiotic agent like rain water alongside biotic agent like butterflies for their pollination (Aguiar *et al*., 2012). As in this mode of pollination orchids do not need to attract pollinators, they also do not need to produce nectar, aroma or attractive floral structures, so the plants can invest all of their energy into making lots of pollen in order to ensure their pollination.

3.2.2. Biotic mode of pollination:

In this case pollen grains are transferred by living pollen vectors (termed as 'pollintors'). According to different types of pollinators, pollination can majorly be divided into 9 categories (Barrows, 2011). These categories are termed as Melittophily (pollination by bees), Psychophily (pollination by butterflies), Phalaenophily (pollination by moth), Myophily (pollination by flies that feed on nectar and pollen as adults), Sapromyophily (pollination by flies that normally visit dead animals or dung for breeding), Cantharophily (pollination by beetles), Malacophily (pollination by slugs and snails), Ornithophily (pollination by birds), Chiropterophily (pollination by bats). In order to reproduce, most orchid species depend on biotic pollen vectors (Henneresse and Tyteca, 2016). Orchids attract their pollinators either by rewarding them or by deceiving (non-rewarding) them.

3.2.2.1. Rewarding pollination:

Orchids lure their pollinators by providing rewards such as protein-rich pollen, nectar, floral oils, lipids, floral parts etc. However, nectar is the most common reward. Nearly about half of the approximate 18,500 species of orchids award nectar and secretions to their pollinators (Tang *et al.*, 2014). Bumblebees pollinate *Galearis diantha* (Schltr.) P. F. Hunt while foraging the flower (Sun *et al.*, 2011). *Bulbophyllum ambrosia* (Hance) Schltr. lure insects by emitting fragrance and providing nectar. Honeybees are the most effective pollinators of *B. ambrosia* (Chen & Gao, 2011). A species of wild mountain mouse, *Rattus fulvescens* is attracted by the odor and coloration of the flower of *Cymbidium serratum* Schltr. While eating the flower's labellum as food these mice eventually pollinate the flower (Wang *et al.*, 2008).

3.2.2.2. Non-rewarding pollination:

This mechanism is also known as deceptive or fraud pollination mechanism as in this case orchids do not provide any kinds of rewards to their pollinators. There are about 6500 orchid species present among 7500 deceptively pollinated angiosperms (Jersáková *et al.*, 2006). According to the reviews of Jersáková *et al*. (2006) and Tang *et al*. (2014) the deceptive pollination mechanism in orchid can be divided into general food deception, brood-site imitation, batesian mimicry, green-leafvolatile imitation, volatile organic compound emission, shelter imitation, pseudoantagonism, rendezvous attraction, and pseudocopulation.

3.2.2.2.1. General food deception:

Around 38 genera of orchid species show general food deception mechanism of pollination utilizing the inborn behavior of food foraging of the pollinators. Nearly, one-third of all orchid species accomplish pollination through food deception (Ramya *et al*., 2020). In this case, the orchids lure their pollinators by expressing the most common floral signals similar to that of other rewarding plant species. These floral signals include pattern of inflorescence, fragrance and coloration of flowers, spurs, nectar guides and pollen-like pappilae (include pigments or function as osmophores and likely to represent visual or tactile signals that guide pollinators into flowers). Often non-rewarding orchids can be observed in close proximity with nectariferous co-flowering species and thus they get the profit of being pollinated. Because of the presence of these rewarding co-flowing plants, a significant amount of increment in the number of pollinators can be observed in the local habitat of these orchids. The orchids that show general food deception have pollinators who are recently appeared or evolved insects, immigrants, or exploratory pollinators having scarce food supply (Jersáková *et al*., 2006).

Cypripedium tibeticum exhibits dark floral coloration, swollen trap-like labellum and emit ethyl acetate (a "minor floral fragrance compound") with sweet fruity odor (Li *et al*., 2006). Pollinators are attracted through pseudopollens or false anthers mainly found in the genera *Polystachya*, *Maxillaria,* some species of *Eria* and *Dendrobium*. The pollinators of the species of *Polystachya*, *Maxillaria* and *Eria* generally collect the protein and starch rich labellar papillae and trichomes. *Arethusa bulbosa, Pogonia ophioglossoides, Calopogon tuberosus* and *Cephalanthera longifolia* lure pollen-foraging bees by vividly yellow coloured tufts of hairs on the labellum (lip) (Jersáková *et al*., 2006).

3.2.2.2.2. Brood-site imitation:

It has been reported that mainly tropical and sub-tropical orchid species tend to imitate some of the most common places for insects' oviposition like putrefying flesh of dead animals, dung and sporocarp. These orchids emit rotten smells and mimic appearances similar to those oviposition sites by exhibiting dark coloration and some special morphological characters. Mainly Diptera and Coleoptera take part in pollination by this mechanism (Jersáková *et al*., 2006). *Paphiopedilum dianthum* develop several floral morphological traits such as helmet shaped labellum, big dorsal sepal and petals with blackish beads or hair like structures on the surface to deceitfully lure female *Episyrphus balteatus* for laying eggs (Tang *et al*., 2014). Several species of the genera *Pterostylis,* *Paphiopedilum*, *Bulbophyllum*, *Cirrhopetalum*, *Megaclinium*, *Anguloa*, *Masdevallia*, *Pleurothalis* and *Cypripedium* show a kind of pollination trap or trap flower mechanism by providing specially modified floral structures to represent a trap like single-way passage to the flies (mainly) who are attracted by the foul smell and dark dull reddish or brownish coloration of the flowers. The Australian helmet-shaped orchid genus *Corybas* attracts fungus gnats by their dark colored geoflorous flowers which probably imitate the sporocarps of basidiomycetes. In this way while laying their eggs the fungus gnats eventually pollinate the plants. *Epipactis veratrifolia* deceivingly influences female syrphids to oviposit on its labellum. But, alongside deceptive oviposition site this orchid species also provides nectar as reward to their pollinators (Jersáková *et al*., 2006).

3.2.2.2.3. Batesian mimicry:

In the nature it is observed that both 'rare' animals and plants tend to mimic more 'common' species to gain several survivals, ecological or reproductive benefits from their ecosystem. This phenomenon is known as batesian mimicry (Starrett, 1993). In order to accomplish pollination some orchids imitate different features from several common rewarding plant species found in the vicinity (Dafni, 1984). The floral structures and color of *Ajuga forrestii* Diels are imitated by *Hemipilia flabellate* in order to fulfill the purpose of pollination through luring *Anthophora mangkamensis* (Luo and Chen, 1999). Duplicating the appearance of false 'fungus-infected foliage and flowers' *Cypripedium fargesii* Franch. Lures, *Cheilosia lucida* for their pollination purpose (Ren *et al*., 2011). The South African orchid *Disa ferruginea* attract a butterfly species *Meneristul baghia* by mimicking red flowered nectar producing *Tritoniopsis triticea* (Iridaceae) and sometimes orange colored nectar producing *Kniphofia uvaria* (Asphodelaceae) (Johnson, 1994). In a similar manner, in order to achieve effective pollination through batesian mimicry *Paphiopedilum purpuratum* (Lindl.) Stein imitates *Eupatorium catarium* Veldkamp (Liu *et al*., 2004), *Paphiopedilum armeniacum* S. C. Chen & F. Y. Liu imitates *Hypericum beanie* N. Robson (Tang *et al*., 2014) and *Eria coronaria* Rchb. f. imitates *Pittosporum glabratum* Lindl (Shangguan*et al*., 2008).

3.2.2.2.4. Green-leafvolatile imitation:

When plants are mechanically wounded by attack of herbivorous insects, plant tissues release a type of chemical substance known as green-leafvolatiles (GLVs). For example, when caterpillars (*Pieris brassicae)* which are the common prey of wasps, attack and bring damage to the leaves of cabbage then the plant tissues emit GLVs (Ameye *et al*., 2017). *Epipactis helleborine* and *E. purpurata* have been reported to release green-leafvolatiles (GLVs) like hexyl acetate, Z-3-hexenyl acetate, and Z-3-hexen-1-ol, which lure the prey-hunting workers of the social wasps *Vespula germanica* and *V. Vulgaris* (Brodmann *et al*., 2008). Thus during the visits of the social wasps, the purpose of pollination is accomplished in these orchids. Honeybee’s alarm pheromone mimicking chemical substance (Z)-11-eicosen-1-olis emitted by orchid *Dendrobium sinense (white flower having a reddish spot in the center)to lure honeybee-hunting hornet Vespa bicolor*(Hymenoptera: Vespoidea) for purpose of effective pollination (Figure-1) (Brodmann *et al*., 2009).

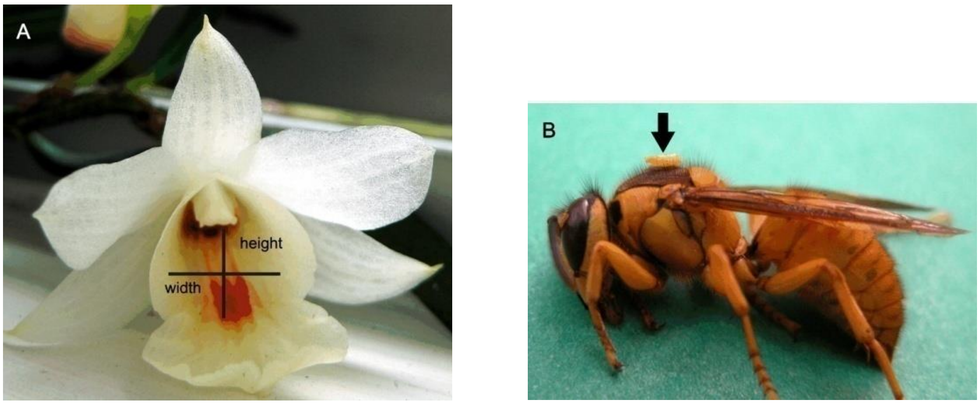


Figure-1: A) appearance of the flower of orchid *Dendrobium sinense; B) Vespa bicolor* hornet with pollen attached on its thorax. (source: Brodmann *et al*., 2009)

3.2.2.2.5. Volatile organic compound emission:

Plant-producing volatile organic compounds (VOCs) exist as a kind of a mixture of low molecular weight lipophilic molecules with low melting points (Dudareva and pichersky, 2006).Volatile compounds produced and emitted by flowers are generally classified into three categories: terpenoids (derived from the 5-carbon compound isoprene) such as Linalool, Geraniol; phenylpropanoids (synthesized by plants from the amino acids phenylalanine and tyrosine) or benzenoids (class of chemical compounds with at least one benzene ring) such as Eugenol and benzyl acetate and fatty acid derivatives such as Methyl jasmonate and jasmonic acid. Flowers of the orchid *Satyrium pumilum* secret a mixture of tissue specific volatile compounds containing sulfurous oligo sulfides such as dimethyl disulfide (DMDS; figure-2) and dimethyl trisulfide (DMTS; Figure-2) which is predicted to provide olfactory signals and lure pollinators such as flesh-eating flies and lepidopterans (Ramya *et al*., 2020).

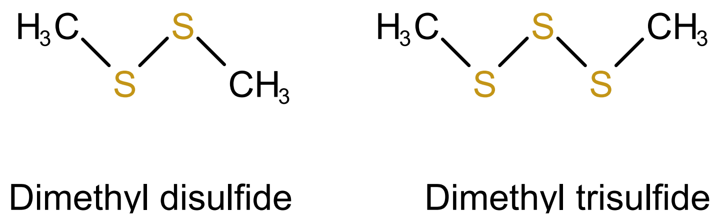


Figure-2: chemical structures of DMDS and DMTS.

3.2.2.2.6. Shelter imitation:

Some specialized floral structures in several orchids provide a kind of temporarily useable shelters to insects by aiding them in case of hiding from predators or escaping from adverse weather conditions. It has been also reported that insects can utilize the flowers for the purpose of thermoregulation, i.e., maintaining their core body temperature, as the floral tube is examined to be 3^{o} C warmer than the temperature of outside environment during day times. An orchid genus *Serapias* having dark reddish floral appearance seems to imitate the dark entranceway to the beehives and provides actual shelter to the insects (Jersáková *et al*., 2006).

3.2.2.2.7. Pseudoantagonism:

While quivering the flowers in the breeze some orchid genera like *Oncidium* and *Tolumnia* possibly become pollinated by some attacking Hymenopterans who show the urge to defend their territory from intruders. In this case the insects often seem to make mistakes to identify among the real intruder and the similar floral appearance of these orchids (Jersáková *et al*., 2006). The flowers of the genus *Oncidium* are pollinated by male *Centris* bees. These flowers provide such a structure which is similar to the enemy insect of male *Centris* bees. So, the male bees always want to drive away intruding enemy insects from its territory. When the bee hits the flower, pollens become attached on the head of the bee. And while visiting the next flower, this bee may deposit the pollens onto the stigma. (https://www.britannica.com/plant/orchid/Natural-history; access date: 21 February, 2021)

3.2.2.2.8. Rendezvous attraction:

When female bees forage for nectar or pollen in the environment, the male bees will try to locate them and copulate with them due to their natural desire for sexual activity (sex drive). Some orchid species including *Cephalanthera rubra* and *Orchis papilionacea* (European) as well as *Disa obtusa* and *Ceratandra grandiflora* (african) mimic the floral appearance and fragrance of these co-flowering rewarding species where the insects generally come and interact. Thus, when the bees mistakenly come to these orchids and involve in their above mentioned mating behavior, they eventually pollinate the flowers (Jersáková *et al.*, 2006).

3.2.2.2.9. Pseudocopulation:

Some orchid flowers have been observed to remarkably imitate female insect's body-shape, size, color and even their sex pheromones (allomones, a mixture of alkenes and alkanes released from one species that put an impact on the behavior of the members of another species). Thus male insects are attracted by the similar appearance, olfaction and tactile sense provided by the flowers. In this way these amorous males get fooled and try to copulate with the flower without any culminating result. This phenomenon is scientifically known as 'pseudocopulation'. Using this method of pseudocopulation orchid flower ultimately gets pollinated (Ellis and Johnson, 2010). Several species of *Ophrys* utilize olfactory, visual/optic and tactile signals represented mainly by highly modified labellum (central petal) to stimulate the sexual behavior of their pollinators. *Ophrys* releases various kinds of odor producing chemical substances (terpenoid, long-chained aliphatic hydrocarbons, aldehydes, ketones, 1-, 2-alcohols, cyclic or aromatic compounds etc.) which produce species specific sex pheromone imitating substance (allomone) by mixing at several concentrations. Males receive the signal of this pheromone like substance through their olfactory receptors present on the antennae. A combined scientific technique of gas chromatography plus electroantennographic detection (GC–EAD), gas chromatography plus mass spectrometry (GC–MS) and different behavioral field tests confirmed the effective pollination method using olfactory cues in the case of *Ophrys sphegodes* and its pollinator bee *Andrena nigroaenea* as well as *Ophrys speculum* and its pollinator wasp *Dasyscolia (Campsoscolia) ciliate.* The flower of mirror orchid *Ophrys speculum* mimics the iridescent darkish purple blue coloration of the glossy wings with UV reflection along with the brownish red body hairs and even eye spots of the female scoliid wasp *Dasyscolia ciliate* (Figure-3). When the males come in contact with the female mimicking flower they can determine the right direction (front and back side) of the female body with the aid of tactile stimuli produced by the orientation of hairs and in this way some pollinators remove the pollinaria by head in a few types of *Ophrys* (head-pollinated, example-*Ophrys sphegodes*; Figure-4) and others with the abdomen in another types of *Ophrys* (abdomen-pollinated, example- *Ophrys lupercalis*; (Figure-4) (Jersáková *et al.*, 2006; Paulus 2006, 2019).

Figure-3: Mirror orchid *Ophrys speculum* mimicking female scoliid wasp *Dasyscolia ciliate*.

(source: Paulus, 2019)

Figure-4: Males of *Andrena nigroaenea* are trying to copulate with head-pollinated *Ophrys sphegodes* (left) and abdomen-pollinated *O. lupercalis* (right), (Photo: H.F. Paulus)

(Source:https://www.researchgate.net/figure/Ophrys-sphegodes-head-pollinated-left-and-O-lupercalis-abdomen-pollinated-right_fig1_224984835; accessed date: 22 February, 2021)

3.2.2.2.10. Trap-pollination mechanism:

Some orchid species trap their pollinators by several specialized floral characters for their purpose of pollination. The genus *Coryanthes* shows a kind of trapping mechanism by evolving special floral structures. While blooming, the sepals and petals of this large flower become folded back and expose the lip. The lip is made up of three segments: upper hypochile (an orbicular- or hood-like structure), middle mesochile (an extended pipe-like structure) and lower epichile (a pail-shaped structure). The epichile contains water lasting for few hours before and after blossoming. The water or fluid is filled inside by two faucet-like organs basally present at the column. Hypochile produce a strong odor which attract the male euglossine bees. These bees come to the flower to transfer the scent in specialized spongy pouches inside their swollen hind legs for launching it into the air while engaging in courtship dancing to attract females. When the males come for the odorous substance they often fall into the water filled bucket. Steep, waxy inner wall with downward-facing slippery hairs does not allow the bee to climb out from this bucket. The bee can only come out from this trap by using a small grippy tunnel made up of the apex of column and epichile of the lip. A constriction is applied through the spout by the flower. Thus, while forcefully exiting the tunnel, the thorax of the bee is rubbed against the pollinia (coherent mass of numerous pollen grains) of this orchid and in this way the pollen grains get attached onto their thorax. As this bee visits next flower it falls again into the trap and while escaping the pollinia carried by the bee may be deposited onto the stigma. (https://en.wikipedia.org/wiki/Coryanthes#cite_ref-2; accessed date: 21 February 2021)
(https://www.britannica.com/plant/orchid/Natural-history; accessed date: 21 February 2021)

3.3. Co-evolution:

According to D.H. Janzen (1980), "Coevolution may be usefully defined as an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first." In case of orchid the concept of co-evolution seems to be the most prominent in long-spurred Madagascan orchid *Angraecum sesquipedale* and long tongued hawkmoth *Xanthopan morgani praedicta* (Figure-5). Observing 33 cm long nectar spur in this orchid Darwin predicted about a moth with long proboscis as the pollinator. Later, his prediction has proven to be correct when *Xanthopan morgani praedicta* was discovered by scientists (Netz and Renner, 2017). In order to decrease competition between pollinators, prevent extravagance of pollens, and achieve the greater chance of effective pollination in plants, both the orchid and its pollinators develop some specialized characters through continuous evolution and thus they gradually urge to establish 1: 1 (obligatory) relationship between themselves (Janzen, 1980). These simultaneous events of evolution between plant and its pollinator can be describes as the core idea of co-evolution.

Figure-5: The long spurred Madagascar star orchid *Angraecum sesquipedale* and its pollinator the hawk moth *Xanthopan morganii praedicta* with its long proboscis.

Image Source: https://cdn.britannica.com/01/150201-050-BCB7094F/Xanthopan-morganii-praedicta-proboscis-star-orchid-Madagascar.jpg (accessed date: 22 February, 2021)

Alongside the benefits, there are few disadvantages that also come along with co-evolution of hawk moth and star orchid. From the reference of Ardetti *et al.* (2012) these can be described as follows:

i) Due to long proboscis length, it will take time to insert as well as retract the entire proboscis during the collection of nectar. This particular fact will make the insect more vulnerable to their predators. Thus decreasing their chance of survivability.

ii) To develop and maintain such a long proboscis, they need to invest more energy than similar other insect species. Thus producing a disadvantage in competition.

iii) Physical friction will also be increased while interacting with the environment (e.g.: flying, foraging or, hovering through congested environment, escaping from predators etc.)

Thus, although this progressive evolution of long proboscis helps to keep up the exclusive 1:1 relationship between the Long-spurred Darwin's star orchid (*Angraecum sesquipedale*) and hawkmoth *Xanthopan morganii praedicta,* it will bring some life threatening disadvantages for the insect.

4. Diverse pollinators of orchids:

Orchids lure largely diversified group of pollinators for achieving effective pollination utilizing various fascinating mechanisms. Mainly insects such as bees, wasps, butterflies, moths, flies, beetles, thrips are considered as well known pollinators of orchids. Except these sometimes birds and rodents are also reported as effective pollinators. By studying, comparing and analyzing different books, online articles and research papers we gather and finalize several data on Indian orchids, their distribution and their pollinators in the following table 1.

Table 1: Habitat and distribution of Indian orchids and their pollinators.

Orchid species	**Distribution**	**Habitat**	**Pollinator**	**IUCN category of orchid**	**Reference**
Vanda coerulea	Mizoram	Epiphytic	Insects of order Hymenoptera, i.e., *Andrena parvula, Lasioglossum* sp., *Xylocopa (Biluna) nasalis* (carpenter bees).	Endangered	Buragohain and Chaturvedi, 2016 De and Singh, 2015
Renanthera imschootiana	Mizoram and neighboring areas in North-East	Epiphytic	fleabeetles, (*Altica* spp.); order: Coleoptera; family: Chrysomelidae.	Endangered	De and Singh, 2015

	India				
Paphiopedilum hirsutissimum	Mizoram	Terrestrial and lithophytic	Hoverflies: *Allobaccha* sp.; *Episyrphus* sp.	Vulnerable	Pemberton, 2013 De and Singh, 2015 Shi *et al*. 2009
Paphiopedilum villosum	Mizoram	Epiphytic and lithophytic	Hoverflies: *Betasyrphus* sp.; *Episyrphus* sp.; *Syrphus* sp.	Vulnerable	Kumar and Rankou, 2015 Liu *et al*., 2009 Pemberton, 2013 De and Singh, 2015
Spiranthes sinensis	Nagaland, Western Himalayas , Assam, eastern Himalayas	Terrestrial	the family Apidae (*Apis cerana*, *Bombus friseanus* and *B. grahami*), were observed visiting the white form 12 species in the families Apidae (four species in the genera *Apis*, *Bombus* and *Ceratina*), Halictidae (six species in the genera *Halictus* and *Lasioglossum*), and Megachilidae (two species in the genera *Anthidium* and *Hoplitis*) foraged on the pink form	Least concern	Tao *et al*., 2018 De and Singh, 2015
Orchis sp.	Sikkim, Western Himalayas	Terrestrial	Bumble–bee queens (*Bombus* Latr. spp.) cuckoo bumble–bee females (*Psithyrus* Lep.	Not Evaluated	De *et al*., 2016 De and Singh, 2015

	and Kashmir.		spp.); males of *Eucera longicornis* (L.) (Anthophoridae) many solitary bee species.		Nilsson, 2008
Habenaria spp.	Sikkim	Terrestrial	Hawkmoth (particularly *Panogena lingens*)	Endangered	Pedron *et al*., 2012 De and Singh, 2015 Pollard and Darbyshire, 2004
Tipularia spp.	Sikkim	Terrestrial	*Autographa precationis*, *Ctenoplusia oxygramma, Cucullia convexipennis*, *Protoboarmia porcelaria* and *Pseudaletia unipuncta*.	Not Evaluated	https://goorchids.northamericanorchidcenter.org/species/tipularia/discolor/ **(**accessed date: 2 December, 2020**)** De and Singh, 2015 https://www.fs.fed.us/wildflowers/plant-of-the-week/tipularia_discolor.shtml#:~:text=The%20flowering%20stem%20originates%20from,The%20flowers%20have%20pollinaria. **(**accessed date: 2 December, 2020**)**
Satyrium nepalense	Sikkim and the Himalayas from Simla eastward; also found in the Khasia Mountains, in those of the Deccan Peninsula	Terrestrial	Beetle *Atrichelaphinus tigrina* (Cetonidae), bee pollinator *Amegilla spilostoma*, the bee *Amegilla natalensis,* skipper butterfly, noctuid moth, the hawkmoth *Basiothiaschenkii,* the long proboscid fly *Prosoeca ganglbaueri*.	Not Evaluated	Johnson *et al*., 2011 De and Singh, 2015.

	around Travancore, and in Ceylon.				
Cypripedium himalaicum	The Himalayas, from Uttarakhand to SE Tibet and Sikkim.	Terrestrial	burrowing bees	Endangered	https://www.arenaflowers.co.in/blog/lady-slippers-orchid-flowers-facts-photos-cypripedium-calceolus/ **(**accessed date: 3 December, 2020**).** De and Singh, 2015 https://valleyofflowers.info/flowers-found-in-valley-of-flowers/himalayan-slipper-orchid/ **(**accessed date: 3 December, 2020**).** http://www.flowersofindia.net/catalog/slides/Himalayan%20Slipper%20Orchid.html **(**accessed date: 3 December, 2020**).** https://indiabiodiversity.org/species/show/229457 **(**accessed date: 3 December, 2020**).**
Cymbidium hookerianum	Himalaya of eastern Nepal, Sikkim and Assam in north-eastern India.	Epiphyte	large bumble bees	Vulnerable	http://www.plantsoftheworldonline.org/taxon/urn:lsid:ipni.org:names:625040-1**(**accessed date: December 3, 2020**).** De and Singh, 2015. https://wsbeorchids.org/2018/365-days-of-orchids-day-398-cymbidium-

					hookerianum/**(**accessed date: December 3, 2020**)**
Coelogyne cristata	Their natural habitat extends east from 75 ° longitude in the Garhwal region of northern India, through Nepal, Sikkim, Assam, Bhutan, up to Khasi Hills in northeastern India.	epiphyte and occasional lithophyte	*Hippofioncelerio* L. (Noctuidae, Sphingidae), *Romigiofragalis* Fabr. (Noctuidae)	Not Evaluated	Subedi *et al*., 2011. De and Singh, 2015.
Bulbophyllum careyanum	Global- Bhutan, Mynamar, Nepal, Thailand. India- Arunachal Pradesh, Sikkim, Meghalaya, Uttar Pradesh, West Bengal.	Epiphytic and lithophytic	Flies, wasps, grasshoppers and bees flower visitor, *Drosophila melanogaster* real pollinator.	Not Evaluated	Gonmei *et al*., 2014. De and Singh, 2015 https://www.nrcorchids.nic.in/orchid/orchid_details.php?id=14**(**accessed date: 9December, 2020**)**

Cymbidium grandiflorum	Arunachal Pradesh, Sikkim, Assam	Epiphytic	Large bumblebees (Order: Hymenoptera)	Vulnerable	De and Singh, 2015 De and Medhi, 2014 https://indiabiodiversity.org/biodiv/species/show/258922 [Accessed date: 13 Nov, 2020].
Cymbidium ensifolium	Arunachal Pradesh, Assam.	Terrestrial	*Apis cerana* (Hymenoptera)	Endangered	https://www.nrcorchids.nic.in/orchid/orchid_details.php?id=47[Accessed date: 13 November, 2020]. De and Singh, 2015 Tsuji and Kato, 2010 http://www.orchidsnewguinea.com/orchid-information/species/speciescode/1886 (Accessed date: 13 November, 2020).
Dendrobium aphyllum	From southern, central and north-eastern India, ArunachalPradesh, Assam, Kerala.	Epiphytic in (semi-) deciduous forest, also lithophytic on limestone cliffs.	Hymenopteran insects (bees)	Least Concern	http://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:626817-1#:~:text=persistent%20in%20cultivation.-,Dendrobium%20aphyllum%20flowers%20between%20February%20and%20July%20in%20the%20wild,and%20also%20on%20limestone%20cliffs. (Accessed date: 13 November, 2020). DeandSingh, 2015 Jalal and Singh, 2015 https://natureproducts.net/

					Forest_Products/Orchids/Dendrobium/D.aphyllum.html. (Accessed date: 13 November, 2020). https://www.toskar.org/dendrobium-aphyllum/ (Accessed date: 13 November, 2020).
Paphiopedilum fairrieanum	Arunachal Pradesh, Sikkim, Assam.	Lithophytic	Fly	Critically Endangered	Gurung *et al*., 2019 De and Singh, 2015. https://orchids.fandom.com/wiki/Paphiopedilum_fairrieanum (Accessed date: 18 November, 2020) Raskoti and Ale, 2011
Paphiopedilum venustum	Arunachal Pradesh, Sikkim.	Terrestrial	Hoverfly	Endangered	Gurung *et al*., 2019. De and Singh, 2015. Raskoti and Ale, 2011. Zhang *et al*., 2016.
Paphiopedilum spicerianum	Arunachal Pradesh, Assam, Manipur, Meghalaya, Nagaland, Mizoram.	Terrestrial and lithophytic.	Two hoverflies: *Allobaccha nubilipennis* and *Episyrphus balteatus.*	Endangered	Gurung *et al*., 2019. De and Singh, 2015. Liu *et al*., 2020

Rhynchostylis retusa	Arunachal Pradesh, Odisha, Andhra Pradesh, Assam, Andaman and Nicobar Islands, Meghalaya, Sikkim, West Bengal, Tamil Nadu, Kerala, Karnataka, Madhya Pradesh.	Epiphyte	*Xylocopa violacea*, *Xylocopa aestuans* (order: Hymenoptera)	Endangered	Pant, 2013. De and Singh, 2015. Buragohain *et al*., 2015. Thakur and Dongarwar, 2019.
Arundina graminifolia	Tripura, Assam, Nagaland, Meghalaya, West Bengal	Terrestrial	14 insect species of the order Dipteran (*Episyrphus blateatus*, *Isomyiasenomera*), Hymenoptera (*Megachile yaeyamaensis*, *Thyreus takaonis*), Lepidoptera (*Eurema* spp.), Orthoptera (*Cteniopus sulphureus*) and Thysanoptera (*Thrip* spp.); *Mylabris pustulata*.	Rare	Debnath *et al*., 2016 De and Singh, 2015. Devika and Nagulan, 2018. Pant, 2013 https://indiabiodiversity.org/biodiv/species/show/228837 (Accessed date: 13 November, 2020).

Ascocentrum ampullaceum	Manipur, Andaman, Assam, Sikkim, West Bengal	Epiphyte	Bird	Not Evaluated	Stpiczyńska *et al*., 2011 De and Singh, 2015.
Paphiopedilum insigne	Assam, Meghalaya, Nagaland, Mizoram, Manipur	Terrestrial	Hoverfly	Endangered	Zhang *et al*., 2016. De and Singh, 2015.
Coelogyne corymbosa	Meghalaya, Sikkim, West Bengal	Epiphyte	Bees and wasps	Not Evaluated	Pant, 2013. De and Singh, 2015. Qin*et al*., 2020.
Phaius tankervilliae	Meghalaya, Assam, Andaman and Nicobar Island	Terrestrial	Large Carpenter bees (*Xylocopa violacea)* Order**:** Hymenoptera	Endangered	Pant, 2013 De and Singh, 2015.

5. Conclusion:

From 65 Million years ago shortly after the mass extinctions at the Cretaceous-Tertiary boundary, the dramatically radiated monocotyledonous family of Orchidaceae which is one of the largest families of angiosperms, have shown much diversified reproductive mechanisms during self and cross- pollination. From very beginning of the period of Darwin, throughout 1930s-1960s and till today diligent studies on orchid pollination have revealed the evidence of utmost entomophily in case of pollination. It can be observed from above discussion that in case of several orchids, a single species is pollinated by diverse groups of pollinators. This is termed as facultative or, generalized pollination. Whereas, other species show species specific pollination (i.e. 1:1 relationship) which is known as obligate pollination. So, in case of facultative pollination the requirement of production of pollen grains and nectar is higher than that of obligate pollination. Thus, energy budgeting as well as the chance of wastage of pollen grains is higher in case of facultative pollination. However, in case of obligate pollination, if either the pollinator species or the plant species becomes extinct then there will be a major chance of extinction of either species. In order to avoid higher energy budgeting and interspecific competition between pollinators and to increase the overall chance of pollination, several orchid species along with their pollinators have promoted the process of co-evolution to maintain 1:1 relationship. There are very few works have been reported in the field of pollination of orchids while there are several researches available on the aspects of diversity, distribution, conservation, morphology, taxonomy and also pharmacological as well as ornamental significance of orchids. Due to habitat fragmentation, habitat destruction, pollution, climate-change and many other human activities, several ecologically and commercially important orchid species are gradually becoming endangered or even critically endangered in India. So, in order to conserve them properly, we must need to know about the pollination biology as well as pollination ecology of those orchids. Considering these aspects we should study about plant-pollinator interactions by emphasizing floral phenology; general plant and animal (pollinators) taxonomy and their morphology; foraging behavior of animals (pollinators); pollination syndrome and sophisticated instrumentation technology like electrophysiology, genomics, chemoecologic and proteomic for determining how the floral features are helpful in attracting the pollinators.

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